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Force adaptation transfers to untrained workspace regions in children Evidence for developing inverse dynamic motor models

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Abstract When humans perform goal-directed arm movements under the influence of an external damping force, they learn to adapt to these external dynamics. After removal of the external force field, they reveal kinematic aftereffects that are indicative of a neural controller that still compensates the no longer existing force. Such behavior suggests that the adult human nervous system uses a neural representation of inverse arm dynamics to control upper-extremity motion. Central to the notion of an inverse dynamic model (IDM) is that learning generalizes. Consequently, aftereffects should be observable even in untrained workspace regions. Adults have shown such behavior, but the ontogenetic development of this process remains unclear. This study examines the adaptive behavior of children and investigates whether learning a force field in one hemifield of the right arm workspace has an effect on force adaptation in the other hemifield. Thirty children (aged 6–10 years) and ten adults performed 30° elbow flexion movements under two conditions of external damping (negative and null). We found that learning to compensate an external damping force transferred to the opposite hemifield, which indicates that a model of the limb dynamics rather than an association of visited space and experienced force was acquired. Aftereffects were more pronounced in the younger children and readaptation to a null-force condition was prolonged. This finding is consistent with the view that IDMs in children are imprecise neural representations of the actual arm dynamics. It indicates that the acquisition of IDMs is a developmental achievement

and that the human motor system is inherently flexible enough to adapt to any novel force within the limits of the organism's biomechanics.

Keywords Development · Motor control · Motor learning · Sensorimotor adaptation · Human

Introduction

Recent systems neuroscience research on goal-directed action in adult humans and nonhuman primates suggests that a neural representation of the limb dynamics, a so-called inverse dynamic model (IDM), forms the basis of voluntary motor control. The basic operation performed by an IDM is to transform planned kinematic trajectories into appropriate patterns of muscular enervation (Jordan et al. 1994; Kalveram 1992; Wolpert et al. 1995). In this context, the notion of a *model* implies that an abstract rule of the limb dynamics is acquired rather than a look-up table that stores the mere associations between an experienced force and the visited space. If IDMs contain exact estimations of the limb dynamics, they can function as ideal controllers (see Fig. 1c). This ability is advantageous for the motor system. It does not have to alter its motor plan once external forces are imposed, because the IDM controller can adapt to changes in limb dynamics.

Evidence for IDMs comes from studies that expose human adults to an unknown force field while they attempt to execute goal-directed arm movements (Gandolfo et al. 1996; Shadmehr and Mussa-Ivaldi 1994). In this situation, humans reveal their ability to extrapolate the dynamics of previously unvisited portions of the workspace. They perform accurate movements to targets that they have not visited before and show so-called *transferred aftereffects*: After removal of the applied force-field, the arm trajectories reveal an overshoot in the opposite direction of the force. Such an effect is found not only in the trained regions of the workspace, but also in its untrained portions (hence the

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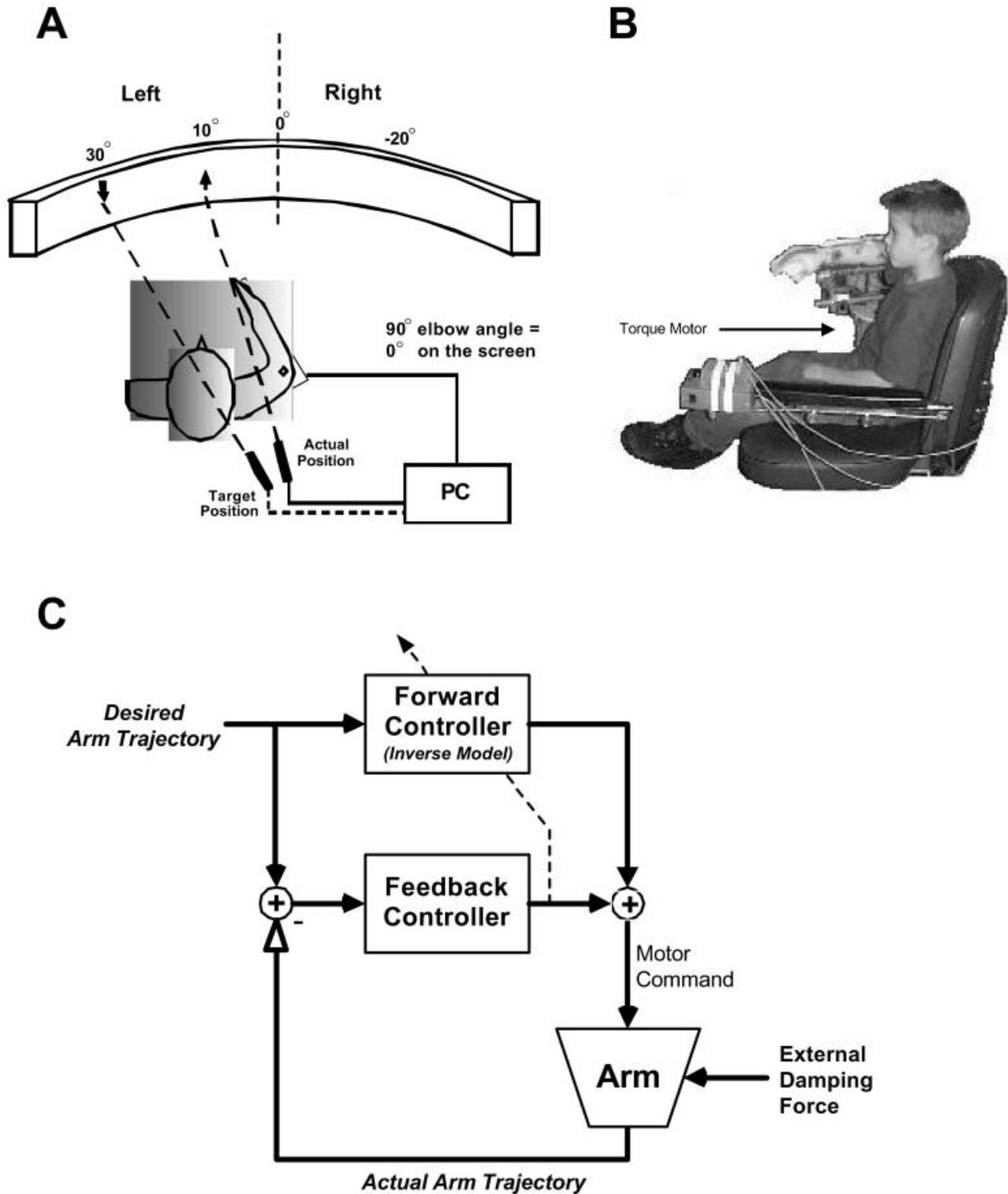


Fig. 1 **a** Experimental setup. Subjects viewed two arrows on a screen in front of them. The top arrow indicated actual arm position, which was visible continuously throughout a trial. The bottom arrow represented the target. Subjects were asked to match both arrows, by performing a flexion movement of their forearm. A torque motor was mounted underneath the elbow joint axis exerting a damping force in specific trials. **b** Side view of the apparatus showing a 6-year-old child during the task. Note that the arm abduction was approximately 90° . **c** Simplified processing schema

of voluntary human arm motor control. Feedforward and feedback processes operate in parallel, and the neural forward controller is an inverse model of the arm's dynamics. When external forces are changing, the inverse model needs to be adaptive to obtain a close match between desired and actual trajectories. The *dashed arrow* through the forward controller box indicates that feedback error signals can be used to modify the internal parameters of the inverse model

term transfer). Such behavior is typical for an inverse model compensating the arm's dynamics plus the no longer existing external force field (Kawato 1999). It cannot be found in a system that simply stores associations between experienced forces and visited workspace in a look-up table.

In light of the present psychophysical evidence that IDMs serve as neural feedforward controllers, the question arises of how and when these internal models are formed in ontogenesis. Infants begin to engage in goal-directed reaching and grasping at about 4–5 months of age (Hofsten 1991; Konczak et al. 1995) and do not exhibit consistent, adult-like kinematics before the age of 2 years (Konczak et al. 1997). This implies that IDMs must have formed during this time period, although we have very little knowledge about the specifics of this developmental process. Our own data demonstrate that children as young as 4 years of age are able to compensate novel external damping forces that they never have experienced before and that they reveal the same type of kinematic aftereffects as adults (J. Konczak, P. Jansen-Osmann, K.T. Kalveram, unpublished work). However, these children were not able to compensate the novel dynamics at the same rate as children in late childhood. These recent findings suggest that the neural representations of limb dynamics in children lack precision. In addition, their path deviations were variable and did not show a systematic error, which indicates that their IDMs are also less stable than in adults. Although these findings are consistent with the notion of a neural IDM as a feedforward mechanism, they do not provide an essential piece of evidence that indicates that indeed the children acquired a “model” of the arm dynamics. If the knowledge of the limb dynamics is local, two scenarios could explain the overt behavior: First, simple associations between visited space and the experienced dynamics were formed and stored in a look-up table. Second, an inverse motor model was acquired. In that case, “rules” were learned that generalized to nonvisited portions of the neighboring workspace. If implicit knowledge of the arm's dynamics is stored in a look-up table, adaptation does not generalize to neighboring workspaces. As a consequence, no aftereffects should be detectable in untrained regions of the workspace after the external damping force is turned off. If a model of the arm dynamics is acquired, aftereffects should be detectable in other parts of the workspace. These aftereffects are called the transferred aftereffects (Shadmehr and Mussa-Ivaldi 1994).

The purpose of the present study is to expand our previous research and to examine whether neural representations of the limb dynamics in children are confined to the visited workspace of the arm or extend beyond these boundaries. If the children's arm kinematics reveal transferred aftereffects, a second piece of evidence would indicate that voluntary motor control in children is indeed based on the formation of an IDM.

Materials and methods

Subjects

Ten adults and 30 healthy children between the ages of 6 and 10 years participated in the study. The sample of children consisted of three age groups, with ten children in each group: 6-year-olds (mean age: 78 months, SD 3.6), 8-year-olds (mean age: 100 months, SD 4.0), and 10-year-olds (mean age: 124 months, SD 4.0).

Children were recruited through advertisements in a local newspaper. Prior to testing, parents gave their informed written consent and answered a questionnaire about motor development of their child. According to these parental reports, none of the tested children had experienced an abnormal or delayed motor development during infancy or early childhood. Except for three children, who were left-handed, the participants were dominant right-handers. The experiment was approved by the local ethics committee and all subjects gave informed consent.

Apparatus

Participants sat in an adjustable chair, facing a concave screen about 1.5 m in front of them. Their right forearms were inserted into an orthosis, which was attached to a lever of a robot manipulator that allowed only flexion-extension movements of the forearm in the horizontal plane. The size of the orthosis was adjusted to each subject's arm anthropometrics to ensure a secure and tight fit. Subjects viewed two illuminated arrows on the concave screen. The “goal arrow” indicated the required target position, a “hand arrow” specified the actual angular position of the forearm. In our setup, 0° angular position corresponded to 90° elbow flexion (see Fig. 1a, b).

Procedure

Prior to movement onset, the subject actively aligned the hand arrow to the goal arrow at -20° or 10° , depending on the respective experimental condition. Subsequently, the goal arrow jumped either to a position of 0° (initial position -20°) or 30° (initial position 10°) on the screen. Thus, two workspaces were defined: a “right” workspace ranging from -20° to 0° , and a “left” workspace ranging from 10° to 30° . Subjects were instructed to perform a goal-directed forearm flexion movement to the respective target position (see Fig. 1a, b). The movement was demonstrated and practiced several times before data collection was started. Reacting as quickly as possible was not emphasized, but the children were told to move accurately and at a quick pace.

During specific trials the torque motor generated a damping force, with the amplitude being proportional to the angular velocity of the subject's arm movement, negative damping. Thus, each time arm velocity was zero (most important at trial onset), no force was acting on the forearm. Furthermore, the alteration of the force condition was perceivable only after the onset of each new block. The damping coefficient was $-1 \text{ Nm}/(\text{°}/\text{s})$. Participants subjectively experienced negative damping as if the arm was pushed in the direction of the intended movement. The torque motor received its input from an amplifier driven by a computer workstation using control software that was based on MATLAB technical programming language.

The blocks consisted of 12 trials each. Five blocks were administered, leading to a total of 60 trials. The experimental procedure is depicted in Fig. 2. Two experimental conditions, determined by the sequence of workspaces moved in were applied. Five subjects of each age group were randomly assigned to one of these conditions. In both conditions, subjects alternately moved in a null-force condition and a force condition with negative damping during one block (12 trials), always starting with a null-force block. In the condition “left workspace first”, subjects first moved in the left workspace. The following blocks were directed “right”-

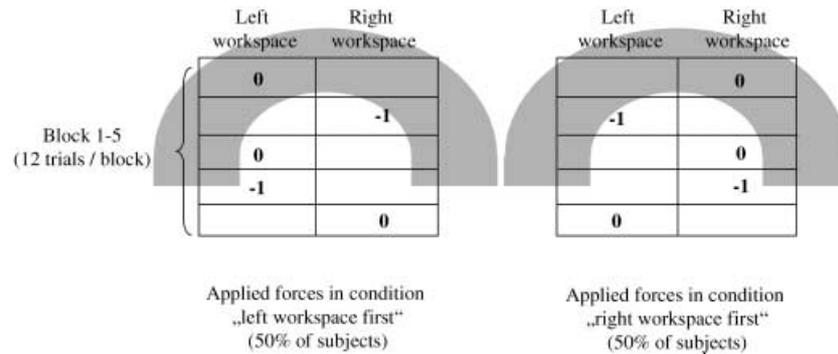


Fig. 2 Experimental procedure. Five subjects of each age group were randomly assigned to one of two experimental conditions. In both conditions, subjects alternately moved in a null-force condition and a force condition with negative damping as long as one block (12 trials), always starting with a null-force block. In condition “left workspace first”, subjects first moved in the left workspace. The following blocks were directed “right”-“left”-“left”-“right”. In the condition “right workspace first”, subjects started moving in the right workspace, followed by the sequence “left”-“right”-“right”-“left”

“left”-“left”-“right”. In the condition “right workspace first”, subjects started moving in the right workspace, followed by the sequence “left”-“right”-“right”-“left”. Thus, adaptation and aftereffects could be investigated in both workspaces (see arrows in Fig. 2), and effects of order of workspace could be controlled.

Forearm inertia was calculated using an anthropometric model based on each subject’s limb length, segment circumference, and total body weight (Clauser et al. 1969; Dempster 1955).

Measurements

Angular position and velocity were measured by a potentiometer and tachometer at the motor shaft for each trial. The data were sampled at 520 Hz and digitized with a 12-bit analog-to-digital converter (Meilinghaus ME300). Digital data were stored on hard disk and then filtered offline with a 2nd-order Butterworth filter with a cut-off frequency of 10 Hz. The length of each trajectory was standardized to 900 samples (ca. 1.7 s). To accomplish comparability between the trajectories, the curves were aligned to movement onset. Movement onset was determined as the time when angular path exceeded 2°. All data preceding the movement onset by more than 100 samples (ca. 190 ms) were discarded.

Basic movement variability

We averaged the trajectories of experimental trials 3–12 for each subject to obtain a measure of the initial performance when no damping force was applied. We termed the resulting mean curve the *baseline* trajectory. Then actual position of each subsequent trial was subtracted from the baseline trajectory for each timed sample. The *absolute* differences were summed over a fixed interval of 800 timed samples, with the interval beginning at movement onset. We will refer to this variable as the trajectory difference score (TD score).

Position error

For each subject, we determined angular position at the end of the first movement unit (i.e., after the first acceleration and deceleration phase) of all 60 trajectories. At this point in time, the transport phase of the reach has ended. It is thus the latest point in the trajectory, where we can reasonably assume that the observed ki-

nematics were the result of feedforward control and were not influenced by the processing of afferent feedback. This angular position value was subtracted from the required target position to obtain a measure of target accuracy.

Statistical analysis

Basic movement variability

Data were analysed using a 1-factorial analysis of variance design with the factor Age (6 years, 8 years, 10 years and adults). The type I error was set to $\alpha=0.05$.

Effects of inertia

Developing children differ in their forearm inertia. To examine whether differences in position error were mediated by differences in moment of inertia, we first computed the mean position error of each corresponding trial over both damping blocks and then determined the correlation between position error and moment of inertia.

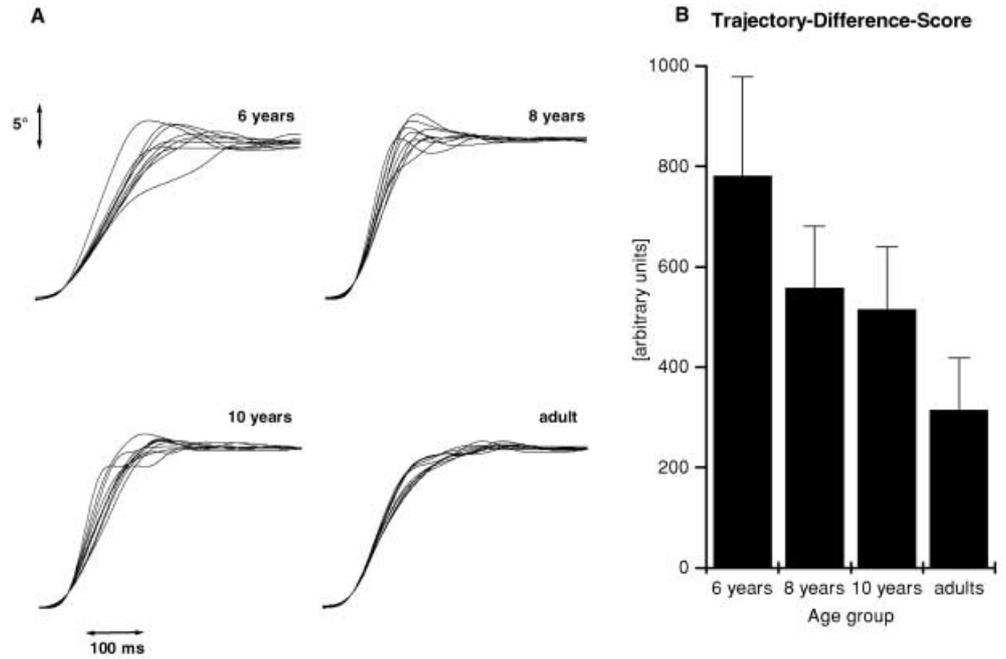
Transition effect

To compute the spatial effect of a transition in external force, we compared the mean position error of the baseline trajectory with the position error of the first trial of each experimental block. Thus, transition effects reflected increments in error due to a transition. Transition effects for the null-force blocks (block 3 and block 5) are transferred aftereffects. Application of a negative force should result in overshoot (positive position error); returning to a null-force block should result in undershooting the target (negative position error). We performed four mixed-measures analyses of variance to examine age (factor Age) and transition effects (factor Transition). To account for multiple testing, critical α was adjusted using the Bonferroni method ($\alpha=0.0125$). Bonferroni post hoc tests of the factor Age were also applied.

Length of adaptation

The change in position error over repeated trials within each block provided a measure of adaptation. Because previous experiments (J.Konczak, P.Jansen-Osmann, K.T.Kalveram, unpublished work) had shown that adaptation in the age groups of this study would normally occur within five trials, the learning curves in each experimental block (blocks 2–5) were computed only for the first five trials. As the result of adaptation, the magnitude of the position error ought to decrease over repeated trials. We considered subjects to have adapted when position error in a certain trial no longer differed significantly from the previous trial. We performed four mixed-measures analyses of variance to examine age effects (factor Age) and the length of adaptation (factor Adaptation). To account for multiple testing, critical α was adjusted using the

Fig. 3 a Trajectories during the first trial block (no force). Trajectories of one subject per age group. Note how spatial variability decreased with increasing age. **b** Mean trajectory difference score of the baseline trajectory. Error bars 1 SD



Bonferroni method ($\alpha=0.0125$). Subsequently, Bonferroni post hoc tests of the factor Age were applied to determine which age group was different from the rest.

Results

Basic movement variability

The baseline trajectories varied considerably dependent on the age of the participants. Exemplar data from one subject of each age group are shown in Fig. 3a. The main effect for Age on movement variability ($F_{3,36}=18.3$, $P<0.0001$) was significant. Subsequent post hoc analysis revealed that the 6-year-old children exhibited a higher initial variability (when no external force was applied) than the older children; all children were more variable than the adults (Fig. 3b).

Effects of inertia

The resulting coefficients of the correlation between position error and moment of inertia were not significant. Thus, we could be reasonably assured that differences in forearm inertia had no particular effect on the observed position error.

Transition effect

The exemplar data shown in Fig. 4 illustrate that the application of a negative force resulted in overshooting, returning to a null-force block in undershooting of the target.

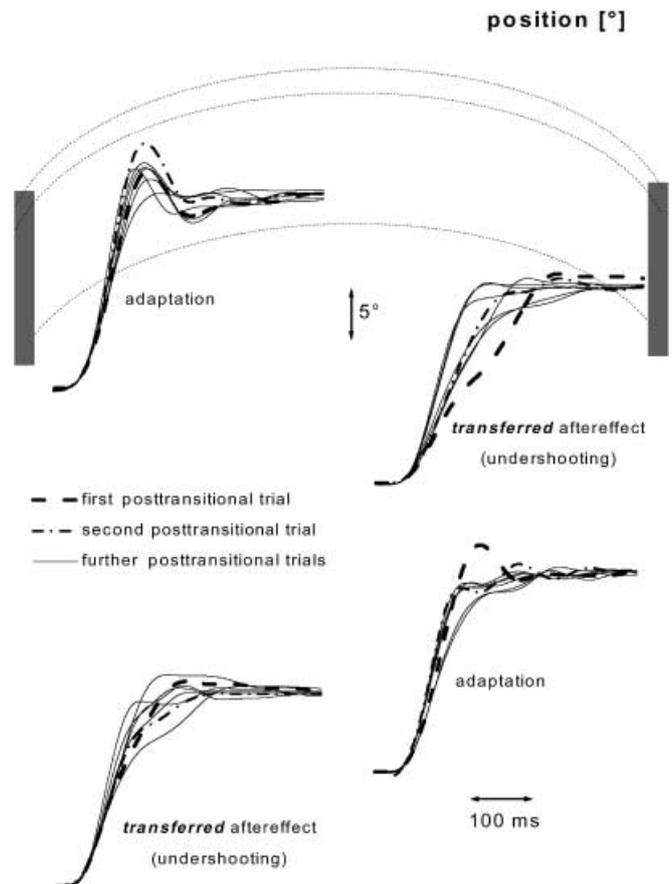


Fig. 4 Exemplar position-time curves during different applications of force. The data of an 8-year-old child during the last 4 blocks (blocks 2–5). Application of the negative damping force (blocks 2 and 4) resulted in an overshoot of the target, returning to a null-force block (blocks 3 and 5) in an undershooting. Note how the curves begin to assume the shape of the baseline trajectory after repeated trials

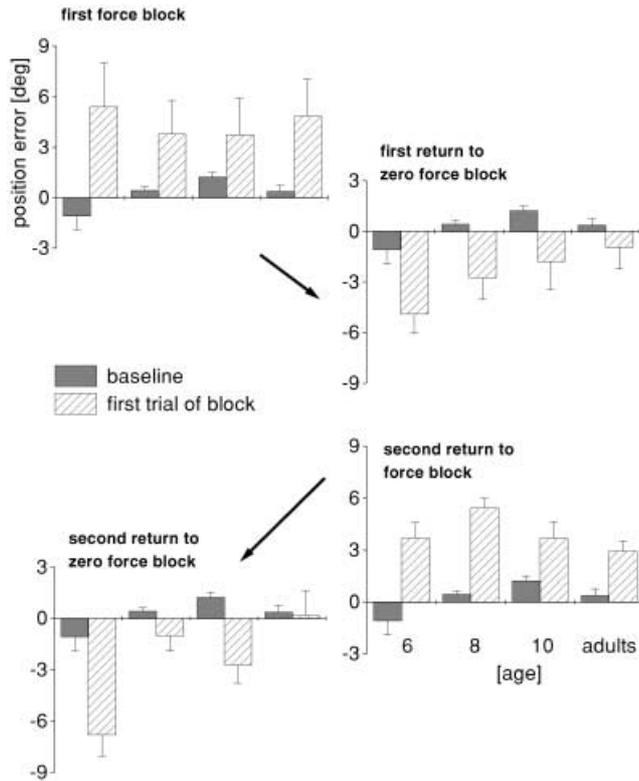
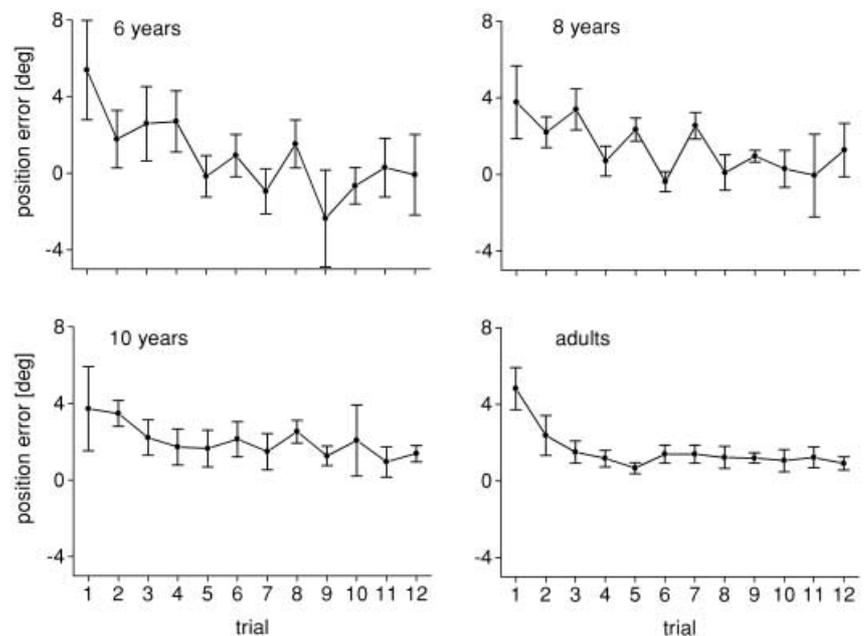


Fig. 5 Transition effects for each experimental block and age group. In the first trial of the two force blocks, where damping was applied, all subjects exhibited overshooting (positive position error), when compared with the mean error of the baseline trajectory. At the first return to a null-force, all subjects showed undershooting (negative position error). At the second return to a null-force block, all children groups showed significant undershooting, but not the adults

Fig. 6 Age group means and standard errors of the position error for all 12 trials in the first block with damping (block 2)



Application of a damping force

The application of a negative force resulted in a significant increase in positive position error when compared with the error of the baseline trials. Significant main effects for Transition were found both in the first and second application of a block with a negative force (effect for Transition for block 2: $F_{1,36}=14.3$, $P<0.001$; for block 4: $F_{1,36}=59.4$, $P<0.000$). There were no age group differences.

Returning to a null-force block

In both null-force blocks, we found significant transferred aftereffects. The return to a null-force block resulted in significant undershooting, that is, a negative position error compared with the baseline error (effect for Transition for block 3: $F_{3,36}=18.98$, $P<0.000$; for block 5: $F_{3,36}=20.69$, $P<0.000$). We found a significant effect of age for block 5, returning to a null-force block (effect for Age for block 5: $F_{3,36}=7.45$, $P<0.001$). Subsequent post hoc tests revealed that the position error of the youngest children was higher than that of the other groups, when returning to the null-force condition for the second time. Adults, in contrast to children, showed no difference between the mean baseline error and the error of the first trial in the last block. Figure 5 shows how the position error changed during a transition with respect to the baseline position error. The data represent the mean error of each age group for each block.

Length of adaptation

Application of a damping force

All participants adapted to the damping force condition. Fig. 6 shows how the position error decreased in the

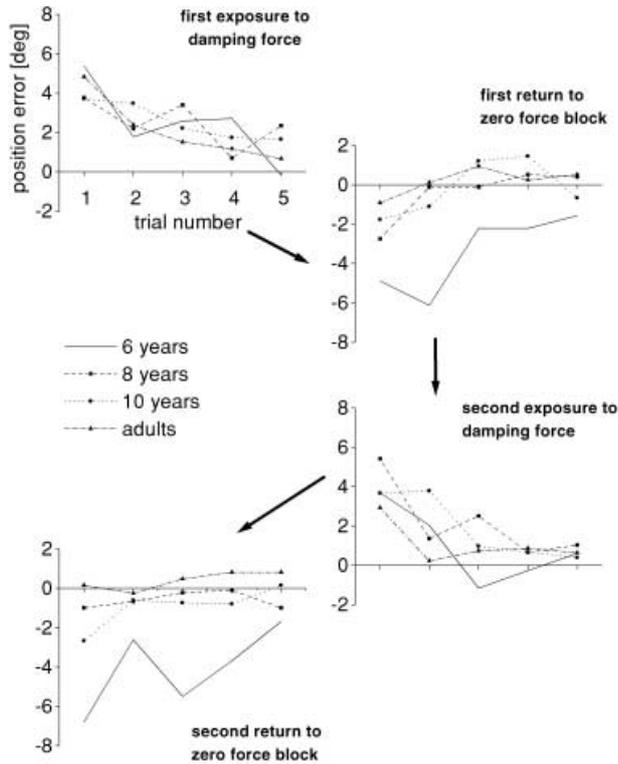


Fig. 7 Change in mean position error as a function of force application during the first five trials of each block. Learning curves are shown for each age group. For the first and second application of the damping force, all subjects showed overshooting only during the first and second trial within each block. At the first and second return to a null-force block, the spatial error decreased within one or two trials except for the 6-year-olds, who needed five trials for adaptation

second block (first exposure to damping) over repeated trials. It is evident that the position error decreased from the first to the last trial and that the standard error was highest in the youngest children.

In the first force block, adaptation was completed after three trials, in the second force condition block, after two trials (effect for Adaptation for block 2: $F_{4,144}=4.58$, $P<0.002$; for block 4: $F_{4,144}=13.68$, $P<0.000$).

Returning to a null-force block

In both null-force blocks, we found significant age effects (effect for Age for block 3: $F_{3,36}=6.52$, $P<0.001$; for block 5: $F_{3,36}=8.29$, $P<0.000$). A Bonferroni-adjusted post hoc test revealed that the six-year-old children were different from the other groups. Except for the youngest children, the participants needed one (block 3) or two (block 5) trials to readapt to the null-force condition. The youngest age group needed five trials to adapt (effect for Adaptation for block 3: $F_{4,144}=7.0$, $P<0.000$; for block 5: $F_{4,144}=3.4$, $P<0.011$). Figure 7 shows the change in mean position error as a function of force application during the first five trials of each block. Note that during readaptation the youngest children revealed the largest position error.

Discussion

Evidence for an inverse dynamics model: children showed transferred aftereffects

All adults and children adapted their forearm movements to changes in the externally imposed negative damping force (see Figs. 4, 6). When returning to a block of trials with no damping, the spatial error was in the opposite direction of the previously applied force. That is, applying a negative damping force led to overshooting, removing it led to undershooting. Because removing the force field was coupled with a change in workspace, the observed aftereffects were *transferred aftereffects*. All children and adults showed these transferred aftereffects. The fact that we found aftereffects in the previously untrained hemifield provides further evidence that children indeed acquired an IDM. Such evidence for a transfer of learning is crucial for the notion of an IDM. Transferred aftereffects demonstrate the organism's ability of generalized learning, an ability that is hard to explain by an associative learning process that connects visited space with the experienced damping force. Yet, this finding is compatible with the idea that humans use a neural representation of the arm dynamics for the control of their upper extremities.

A possible caveat of interpreting our findings within an internal model framework is that the considered force field was velocity-dependent, while transferred aftereffects were position-dependent, being only observed in different portions of the workspace. Hence, one might argue that an investigation of true generalization would require moving at novel velocities and examining appropriate aftereffects in arm or hand velocity. In the present experiment, the hand velocity profiles changed initially when exposed to a new damping force, but they did not differ between workspaces. Thus, a faulty mapping between joint velocity and applied external torque could also cause transferred spatial aftereffects – an interpretation in line with associative learning theory. However, recent research has shown that adaptation to changes in movement dynamics is independent of the executed kinematics during adaptation (Conditt et al. 1997), lending credibility to the notion of a neural module that learns to reproduce the structure of the environmental field as an association between visited states and experienced forces. In light of these controversial findings, we would still argue that our findings and previous experimental evidence support the notion of neural IDMs. However, in all fairness, we also see that our psychophysical data cannot totally refute the notion underlying associative learning mechanism.

The ability to quickly readapt develops with age

Children found it more difficult to readapt to a null-force environment than the adults. This was especially true for the youngest children. Our data demonstrate a clear de-

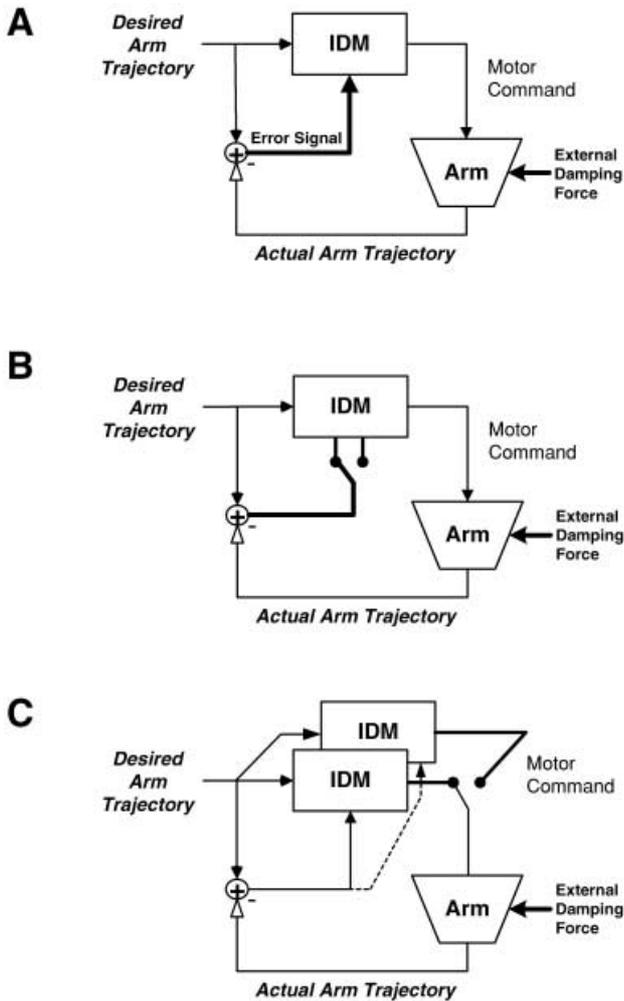


Fig. 8a–c Three possible scenarios for updating inverse dynamics models after changes in external forces. Here, the error signal used for updating inverse dynamic models (*IDM*) is derived from a feedback controller (see Fig. 1c). Alternative sources for an error signal that are based on the input of a forward model have been suggested for grip force control

developmental effect in the ability to readapt, which was especially prominent after the first return to a null-force (block 3). Here, the mean position error decreased with increasing age. Upon the second return to a block with no damping (block 5), the 6- and 10-year-olds did not show any improvement within the first trial, while adults were able to return to their initial baseline level. The 6-year-olds exhibited the slowest learning rates. Figure 7 illustrates that, as a group, the 6-year-olds were not only most affected by the change to a null-force, but also needed more time to return to their previous level of performance. Even after five trials, some of them had not fully readapted. These performance differences between age groups cannot be explained by differences in arm inertia, given that the correlation between position error and arm inertia was not significant.

What can account for the developmental differences in readaptation?

Three explanations might account for these observed developmental differences in readaptation. First, the assumption is made that only one *IDM* exists in the brain that is continuously updated if the dynamics of the lever arm system change (Fig. 8a). In that case, the neural process of updating is simply faster in adults and, during childhood, processing speed increases with increasing age. Such a scenario implies that the neural networks responsible for readaptation become more efficient during ontogenesis. Improved efficiency might be explained by an increased ability to update synaptic weights. These synaptic weights refer to those nodes of the network responsible for compensation of external forces (e.g., damping forces). This interpretation is supported by the observation of exponential learning curves (Kalveram 1992). Second, one *IDM* could have two parameter inputs, one for each applied force (Fig. 8b). If this is correct, readaptation would require fast and precise switching between both inputs. In this case the ability to switch between input channels would improve with increasing age. The third alternative assumes that several *IDMs* representing different dynamics are formed in the brain and can coexist at least for a limited amount of time (Fig. 8c). In this interpretation, adults show a superior rate of adaptation, because their memory trace of the null-force *IDM* is temporally more stable and a more precise representation of the actual limb dynamics. In contrast, the *IDMs* of children are less stable, and learning another *IDM* – to compensate for the new damping force – interferes with the retention of the existing inverse model. This implies that both *IDMs* compete or share the same network resources, and/or the neural representation of original *IDM* was a less precise model of the true arm dynamics.

Support for this third view comes from the results of several psychophysical studies with adults. They show that subjects are able to move in different force fields without interference when the learning of the two fields is separated in time by at least 5 h. That is, stable and precise representations of two different *IDMs* can be retained in parallel (Shadmehr and Brashers-Krug 1997). This observation is in agreement with the theoretical notion of multiple paired inverse and forward models responsible for different contexts (Wolpert and Kawato 1998). What seems unclear, at the moment, is how many *IDMs* can coexist in the brain at any given time. This question has important theoretical implications for the concept of internal motor models. If the number of potential motor models in the brain becomes seemingly endless, the concept cannot be falsified and might simply become another metaphor for a stored representation of movement. Thus, it is imperative to demonstrate that the basic processes of motor adaptation are rule-based. A systematic analysis of children's and preferably infants' movements can provide insights into how and when these rules are acquired in ontogenesis.

Conclusions

In conclusion, the results of this study in combination with our previous work provide evidence that the motor systems of children use IDMs to control their arm motion. Knowing that the children had similar difficulties in force adaptation and readaptation to a null-force indicates that there is no innate predisposition to adapt to a specific force field (i.e., the force field that we are exposed to in daily life). The lack of precision of movements in early childhood can be explained by imperfectly tuned parameters within these models. Finally, adequate and fast motor adaptation to externally imposed forces is not achieved in early childhood but through a developmental process that lasts at least until late childhood.

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